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OVIPOSITION AND EMBRYONIC DEVELOPMENT IN THE VOLUTID
SNAIL ADELOMELON ANCILLA

Soledad Zabala1*, Andrés Averbuj!, Carlos Sanchez Antelo2, Pablo Е. Penchaszadeh? & Gregorio Bigatti1,3

ABSTRACT

Intracapsular embryonic development is common in marine gastropods. In many species, embryos obtain nutrition during ontogeny by ingesting substances contained in the intraca-psular fluid. South American volutids spawn egg capsules containing relatively few eggs, and development is entirely intracapsular, with young hatching as crawl-away juveniles. The spawning habits, egg capsules morphology and embryonic development of the South American volutid Adelomelon ancilla is described in this work. Egg capsules of A. ancilla (n = 42) contained 3.0 + 1.4 (mean + SD) embryos with a range of 1-6 eggs or embryos. The embryonic morphological changes and body spiralization occur simultaneously with embryo feeding. All embryos within a single egg capsule shared the same developmental stage. No evidence of cannibalism or intracapsular competition was found, suggesting that food is not a limiting resource as in other volutid species. Estimated intracapsular developmental time varied between five and six months (between 12-14°C). The long developmental time and low number of embryos inside the egg capsules, together with late reproductive maturity and longevity of adult individuals, reinforce the statement that the neogastropod Adelomelon ancilla
is a fragile resource that must be conserved in Argentinean benthic communities.
Keywords: Neogastropoda, Volutidae, Patagonia, egg capsules, intracapsular develop-
ment.

INTRODUCTION

Intracapsular embryonic development is
common in marine gastropods. All neogas-
tropods lay egg capsules that protect their
embryos, however, little is known about the structure, composition and intracapsular fluids ofthese capsules (D’Asaro, 1988; Miloslavich, 1996a, b; Rawlings, 1999; Bigatti et al., 2014). In many species, embryos ingest substances contained in the intracapsular fluid during development, which provide nutrition during ontogeny.
Little is known about the development of the family Volutidae, with the exception of some recently studied South American spe-cies (Penchaszadeh & De Mahieu, 1976; Penchaszadeh et al., 1999; Penchaszadeh & Miloslavich, 2001; Penchaszadeh & Segade, 2009; Bigatti et al., 2014). There are significant differences regarding developmental modes

among volutids, associated mainly with the geographic region they inhabit (Penchasza-deh et al., 1999), always showing a similar pattern within each group. The first pattern, observed in West African volutids consists of the incubation of one spherical egg capsule in a pedal gland. Developing eggs and ~100,000 nurse eggs are present; hatching mode being a shelled veliger (Marche-Marchad, 1968, 1980). The second mode, found in Indo-Pacific and Australian volutids, consists of an egg mass with numerous capsules attached to hard sub-strata. Only a single embryo develops per egg capsule; embryonic nutrition remains unknown (Amio, 1963; Knudsen, 1993). Finally, the third mode observed in South American volutids, in-volves the attachment of large egg capsules to
hard substrata, containing few embryos inside,
with the exception of the free demersal egg
capsules of the volutid Adelomelon brasiliana
(Penchaszadeh et al., 1999). Embryos feed on

1LARBIM - CENPAT — CONICET, Bvd. Brown 2915, U9120ACD, Puerto Madryn, Chubut, Argentina.
2Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” — CONICET, Av. Angel Gallardo 470, C1405DJR, Buenos Aires, Argentina.
3UNPSJB, Universidad Nacional de la Patagonia San Juan Bosco, Bvd. Brown 3100, Puerto Madryn, Argentina. *Corresponding author: zabala@cenpat.edu.ar

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intracapsular proteic liquid and hatch as crawl-
ing juveniles. These species occur in a wide
variety of forms, both in the intertidal and the
subtidal zones. The embryonic development
of these volutids is completed within the egg capsules, without free larval stages (Ponder, 1974; Pechenik, 1986; Miloslavich, 1996a, b; Penchaszadeh & Segade, 2009; Bigatti et al., 2010, 2014). In particular, Adelomelon ancilla (Lightfoot, 1786) was not studied before in respect to its oviposition modality and devel-opmental biology. |
The marine snail Adelomelon ancilla is an edible neogastropod belonging to the family Volutidae, which is distributed along the southern tip of South America, from 35°S (Brazil) in the southwestern Atlantic to Ushuaia in the Beagle Channel (Zabala, 2013), the Malvinas/Falkland islands and northward into the Pacific, reaching central Chile (25°S, Chiloé Island; Castellanos & Landoni, 1992). This species attaches its egg capsules individually to hard substrates, such as empty bivalve shells or stones. Hatching occurs at the crawling stage, after complete intracapsular development while feeding on the intracapsular fluid (Penchaszadeh & De Mahieu, 1976); however, there is no detailed information about its embryonic development. While their gametogenic cycle, diet and popu-lation parameters have been well documented (Penchaszadeh et al., 2009; Zabala et al., 2013a, b), further work is necessary to pro-vide a complete description of intracapsular development. Along the Patagonian shore, A. ancilla inhabits shallow waters (from 5 m depth) on gravels or mixed bottoms and lives most of the time buried in the substrate. This species is a top-predator of benthic communi-ties, preying principally on other gastropods and on bivalves (Zabala et al., 2013a). The oviposition season occurs from July to No-vember (Winter-Spring) and it is correlated with the gametogenic cycle, both related with the photoperiod (Penchaszadeh et al., 2009). In Golfo Nuevo, the water temperature varies from 9.7°C to 18.3°C (Spring — Fall, respec-tively), and the photoperiod varies from 9 to T5n.orlignt
The aim of this work was to study the oviposi-tion, embryonic development, developmental time, egg capsule morphology and structure of Adelomelon ancilla from Patagonian shallow waters. À comparison with other members of the Volutidae family is included.

MATERIALS AND METHODS

Sampling in Patagonian Shallow Waters

Field samples and observations were made monthly from March 2008 to December 2011, in Nuevo Gulf (NG), Patagonia (42°48’S, 64°54’W; Fig. 1). Collection of specimens and egg capsules of A. ancilla were performed by SCUBA diving on mixed bottoms at depths between 6 and 10 m. Bottom water temperature was measured in situ for the same period of time by Dellatorre et al. (2012).

General Features of Egg Capsules

An extensive investigation on the oviposition process and developmental biology of Adelo-melon ancilla from the shallow waters of NG was performed. The substrate of oviposition was recorded for each of 84 collected egg capsules. Diameter (maximum width) and height were measured with a 0.1-mm precision digital caliper for allegg capsules.
In order to determinate the number of layers ofthe egg capsule walls and to assess chang-es throughout the developmental stages, por-tions cut from recently laid egg capsules and at hatching were observed under scanning electronic microscopy (SEM). Samples were first fixed in glutaraldehyde in phosphate buf-fer (pH: 7.4) for 6 h, dehydrated in a graded ethanol series, critical-point dried, mounted and coated with gold in a Denton Vacuum Desk IV. Observation and photography were conducted with a JEOL JSM-6460LV SEM. In order to test if egg capsules were com-posed of a calcareous cover as in other vo-lutids (Bigatti et al., 2010), newly laid capsules were treated with 50% hydrochloric acid to determine if CO, bubbles were produced. In addition, elemental analysis was performed in recently laid egg capsule, fixed as described above for SEM, with the same microscopy equipped with an EDAX PW 7757/78 X-ray energy scattering microanalyser, for standard-less element quantification.

Embryonic Development

Forty two egg capsules were randomly chosen from the total sample and dissected. The number of eggs/embryos per egg capsule was counted under a light microscope, and the intracapsular egg diameter was measured be-

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South America

Atlantic
Ocean

FIG. 1. Sampling site (black dots) of Adelomelon ancilla egg capsules in
Nuevo gulf.

fore cell division whenever possible. Embryos within the egg capsules were classified into one of six developmental stages: 0 (Egg), 1 (Morula/Gastrula), 2 (“Veliger”), 3 (“Pedive-liger”), 4 (Coiling Embryo) and 5 (Hatchling); for a detailed description see Table 1. Total length of the embryos was measured at each developmental stage. In addition, the number of juveniles per egg capsule was counted and measured in all intact egg capsules. All measurements were made with a stereoscopic microscope with a 0.01-mm precision ocular micrometer. Velum size was recorded as the maximum width when expanded. Throughout the study period, 42 egg cap-sules in different stages of development, including stage O (the female was laying the egg capsule at moment of sampling), were collected in NG and maintained in separate conditioned aquaria. Physical parameters included maintenance of salinity at 35 ppm in accordance with field measurements and a photoperiod of 12:12 h light: dark. Tempera-ture ranged between 12 and 14*C (late spring temperature). Total developmental time was recorded.

RESUETS

General Features of Egg Capsules

Egg capsules measured an average of 32.54 + 4.61 mm (mean + SD) in width and 28.80 + 5.94 mm in height (n = 84). Most egg capsules were attached on the concave side (95.2%) of empty shells of the clam Eurhomalea exalbida (92%) or Ameghinomya antiqua (8%), both belonging to the family Veneridae (Figs. 2, 3). Egg capsules were deposited on the convex side of empty bivalve shells only in 4.8% of the cases.
Oviposition was observed in situ during div-ing samplings at NG. The process involved several steps. Initially, the female fastened her muscular foot to the substrate where the egg capsules were eventually laid. Then, the soft egg capsule was expulsed through the vagina of the female, covered with her foot, and eventually attached to the substrate probably by pedal gland secretions. Finally, the female fixed and molded the egg capsule with her pedal gland located on the sole of the foot, giving it shape and rigidity. The egg capsules

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TABLE 1. Embryonic development of Adelomelon ancilla. Values represent mean size + SD and range (parenthesis).

Embryo stage

Egg Round and whitish, before cellular cleavage. Polar body
present.

Morula/Gastrula

“Veliger”

“Pediveliger”
stomach. Incipient foot.

Coiled embryo

Hatchling

Desciption

Roundish embryo with >16 cells.

Embryo with ciliated velum in constant development, mouth and scarce intracapsular fluid into the stomach.

Velum developed, increase of intracapsular fluid into the

Juvenile hatches as miniature adult; calcified shell with violet band colors; egg capsules opening visible

Mean embryos size
(in mm)

0.209 + 0.053 (N = 15)
(0.175-0.220)

0.219 + 0.046 (N = 21)
(0.200-0.240)

1.523 + 0.655 (N = 19)
(0.880-2.730)

3.798 + 0.754 (N = 11)
(1.950-4.850)

Foot completely developed, resorption of velum; presence 9.005 + 1.284 (N = 28)

of shell gland; beginning of anterior shell calcification. (7.100-10.640)

10.386 + 1.074 (N = 47)
(7.500-11.380)

are externally white, large rounded and flat (Figs. 2, 3). The test with HCI was negative for the presence of a calcareous cover of the egg capsule. Furthermore, EDAX analysis of layered egg capsule wall showed only peaks for С and О and was negative for the presence of Mg and Ca element peaks. The minimum shell length of females from NG laying egg capsules was 114 mm.

Each capsule contained 3.0 + 1.4 embryos (mean + SD) with a range of 1-6 or embryos (п = 42). No plug or opercular opening was observed in any ofthe studied egg capsules. The hatching
area ofthe egg capsule was predetermined and
was always observed as a suture line on one
side ofthe egg capsules, close to its bottom. The
egg capsules were composed of different layers
according to their developmental stage. Newly

FIGS. 2, 3. Oviposition of Adelomelon ancilla in the field. FIG. 2: A. ancilla laying an egg capsule onto a bivalve (Eurhomalea exalbida) empty shell; FIG. 3: Egg capsules of A. ancilla deposited in the con-cave portion of empty bivalve (E. exalbida) shell, note the difference in color that corresponds to early (white) and late (translucent) developmental stages. Abbreviations: b: bivalve shell; c: capsule; f: foot; m: mouth; $: shell. Scale bars: Figs. 2, 3 = 1 cm.

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laid egg capsules contained three distinguish-able layers (Fig. 4), whereas those found at late stages of development presented only two lay-ers (Fig. 5). The outer and inner layers appeared amorphous in aspect; meanwhile, the medium layer was observed as a laminar structure (Figs. 4, 5). At the same time, the wall’s thickness of the inner layer varied depending on develop-ment stage. This inner layer was reduced in ad-vanced developmental stages, and completely absent at the hatching stage. At the same time, as embryos grew in size, intracapsular nutrient fluids adhered onto the inner surface of the egg capsule were consumed byj uveniles using their radulae. Macroscopically, the intracapsular fluid was characterized by two components: (1) viscous whitish aggregates in which eggs and embryos were immersed and which made the localization and removal of eggs very difficult. This viscous phase decreased in quantity as the embryo development progressed, giving the egg capsule an increasingly transparent aspect; and (2) an almost transparent liquid, which enabled the observation of the embryos inside the egg capsule.

Embryonic Development

Newly laid egg capsules contained uncleaved eggs that measured 0.209 + 0.053 mm (mean + SD) in mean maximum diameter. Cell cleavage was spiral and holoblastic with the presence of polar bodies (Fig. 6). The next observed stage was offour cells (Fig. 7), followed by the morula stage (Fig. 8) and then a gastrula (Fig. 9). In all these developmental stages, the size remained

approximately the same. The “trochophore” stage was not observed during this study, prob-ably due to its short time of occurrence.
As a general rule, once the “veliger” stage was reached the embryos fed on the intraca-psular fluid continuously, and morphological changes (organ formation and body spiraliza-tion) ensued. The mouth and stomach were recorded at the “veliger” stage in which em-bryos were active, showing both rotational and translational movements produced by velum cilliary currents. This stage was divided into an early and a late “veliger”, each characterized by the presence of a velum of different size, shape and functionality. The early “veliger” velum was an incipient ciliated band at the anterior region (Fig. 10) that corresponded to the cephalic area of the embryo. Meanwhile, the late “veliger” velum was a lobed-shape structure with a band of cilia involved in feeding and mobility (Figs. 11, 12). At advanced late “veliger” stages, the large ciliated velum increased its size and ac-tivity, which produced a current drawing food into the mouth. On the velum area, transparent vacuolar cells (athrocytes) were distinguished (Figs. 11, 12). At this stage, the mouth and vis-ceral mass were clearly observed (Figs. 11, 12), while the body began to appear bottle-shaped. At this stage, the velum size (2.03 mm + 0.011 (mean + SD, п = 19)) was equal or larger than the body mass. On occasion, nutrient particles
were noted in the embryo’s stomach.
At the “pediveliger” stage, a foot began to
develop. The velum reached its maximum
size (2.60 mm + 0.14 (mean + SD, n = 11))
(Fig. 13), and remained active collecting food

FIGS. 4, 5. Egg capsule wall ofA . ancilla by Scanning Electron Microscopy (SEM). FIG. 4: Egg capsule recently laid showing 3 layers; FIG. 5: Egg capsule already hatched presenting only 2 layers. Abbrevia-tions: E: external, I: inner, M: medium. Scale bars: Figs. 4, 5 = 20 um.

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FIGS. 6-19. Embryological development of Adelomelon ancilla. FIG. 6: Egg without cleavage.
Note the polar lobe; FIG. 7: 4-Cell stage; FIG. 8: Morula; FIG. 9: Gastrula; FIG. 10: Early “veliger” stage with incipient velum; FIG. 11: Embryo *veliger” stage with velum developed;
FIG. 12: Embryo “veliger” stage with intracapsular nutrient into the stomach. The velum is expanded and the stomach is visible by transparency. Note the athrocyte cells in the velum;
FIG. 13: Early “pediveliger” stage with intracapsular nutrient in the velum and stomach; FIG. 14: “Pediveliger” stage; note the foot and the shell gland; FIG. 15: Embryo in early coiled-shell stage; the shell gland that secretes the protoconch is visible and the velum began to reabsorb; FIG. 16: Coiled-shell embryo; note that ingestion of intracapsular nutrient (white) is still occurring at this stage; FIG. 17: Coiled-shell embryo presenting spiralization, foot and protoconch developed; FIG. 18: Hatchling; FIG. 19: Egg capsule with crawling juveniles (pre-hatchlings) inside. Abbreviations: ac: athrocytes cells; b: bivalve; c: egg capsule; e: embryos; ey: eye; f: foot; in: intracapsular nutrient; m: mouth; pb: polar body; pr: protoconch; s: stomach, sg: shell gland; si: siphon, t: tentacle, v: velum; vm: visceral mass. Scale bars: Figs. 6, 7 = 100 um, Figs. 8, 9 = 50 um, Fig. 10 = 300 um, Figs. 11-13 = 400 um, Fig. 14 = 500 um, Fig. 15 = 700 um, Fig. 16 = 900 um, Figs. 17, 18 = 1mm, Fig. 19 = 1

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—®-GN Patagonian waters

Tl(oemmtnagl)t h

Egg Morula/Gastrula Veliger

(47)

(28)

(11)

Pediveliger Coiled embryo Hatchling

FIG. 20. Size variation throughout development of Adelomelon ancilla (bars show SD and parenthesis indicate the number of individuals measured (N) for each stage).

that was ingested and then digested in the
stomach (Figs. 13, 14). Associated with this,
the embryonic movements decreased. The
visceral mass size, filled with intracapsular
nutrients, developed faster in relation to the
cephalic region. The shell gland appeared as a scalloped edge on the basis of the cephalic structures (Fig. 13).
The coiling embryo stage was characterized by the presence of a greatly reduced velum (1.28 mm + 0.20 (mean + SD, n = 28)), which was completely reabsorbed by the end of this stage (Fig. 15). Throughout development of the coiling stage, the embryo was observed increasing degrees of external body coiling; late coiling embryo recorded at least one full-turn of the visceral mass. Calcification of the pro-toconch, although still thin and fragile, began at this stage by the shell gland situated on the mantle edge (Figs. 15, 16). The deposition of calcium appeared as an antero-posterior di-rected process, starting at the shell-gland cells which accompanied body growth direction, and finishing at the apex region before embryonic hatching (Figs. 15-17).
The hatchling stage was characterized by the early presence of a fully developed calcified pro-toconch in the embryo, with the occasional and temporary exception of specific small rounded areas on the apical side of the shell (Fig. 17). Hatchling juveniles had the typical white and

pink epidermal pigmentation of the adult clearly visible in the siphon and dorsal side of the foot (Fig. 18). The presence of eyes at the base of the tentacles was also noted. At this stage, the transparent egg capsule wall enabled observa-tion of the embryos crawling behavior (Fig. 19). The presence of the radula could be observed in dissected hatchlings using a stereomicroscope; however, this organ may only be present as an incipient structure in previous stages. For comparison of the embryonic developmental stages sizes see Table 1 and Figure 20.
In general, all embryos that were present within a single egg capsule shared the same developmental stage. Notwithstanding, in a few cases (n = 3 of 42 observed egg capsules), remarkable differences in the total length of em-bryos were observed. Different developmental stages were rarely present in the same egg capsule (7%; n = 4 egg capsules); when this occurred it was most commonly associated with morphological abnormalities in one or more of those embryos.
The development time of embryos in aquar-ium was estimated in 5-6 months at 12-14*C water temperature. This time was calculated integrating the developmental time information from three newly laid egg capsules and other egg capsules (n = 42) collected at different developmental stages and maintained in con-ditioned aquaria until hatching.

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DISCUSSION

General Features of Egg Capsules

Adelomelon ancilla females attach their egg
capsules to a variety of submerged objects (frequently empty clam shells or stones),
which are abundant in the study area and, in the case of some bivalve species, are also part of the species diet (Zabala et al., 2013a). It is remarkable that A. ancilla choose mainly concave surfaces (95.2% of cases) to attach their capsules. Curiously, the sympatric volutid Odontocymbiola magellanica also deposit egg capsules on submerged objects, but always lay them on the convex side (Bigatti et al., 2010). Nonetheless, egg capsules of the two species never co-ocurred on the same empty shell valve. Furthermore, in contrast with O. magellanica (Bigatti et al., 2010), egg capsules ofA . ancilla lack an external calcium carbonate cover. The absence of a calcareous layer may be associated with increased susceptibility of encapsulated embryos to predation (Rawlings, 1999); however, this may be offset by female’s selectivity of (more protective) concave sur-faces for oviposition. Such differences between the two sympatric volutids, both top predators of Patagonian benthic communities (Bigatti et al., 2010; Zabala et al., 2013a), could reflect differ-ential use of the resources, thereby preventing niche overlap (prey and/or habitat use). Gastropod egg capsules are very complex structures; the microstructure is commonly composed of three or four layers (D’Asaro, 1988; Rawlings, 1990, 1994). In A. ancilla, it was arranged in three layers, in concordance with others caenogastropods as the volutids O. magellanica (Bigatti et al., 2010) and Voluta ebraea (Matthews-Cascon et al., 2010), the nassarid B. cochlidium (Averbuj, 2009) and others muricids and buccinids (D’Asaro, 1988; Ojeda & Chaparro, 2004). The inner layer ofA . ancilla egg capsules is reduced and disappears as development advances as reported in other volutids (Matthews-Cascon et al., 2010; Bigatti et al., 2014), mainly as a result of radula action of embryos on the inner egg capsule wall.

Embryonic Development

The embryonic development of Adelomelon ancilla (Volutidae, Zidoninae) is direct, without a free larval stage; thus, embryos hatch as crawl-ing juveniles (Penchaszadeh et al., 1999). After a series of cell divisions with few size changes,

embryonic growth occurs simultaneously with morphological changes, associated with feed-ing of the embryos upon development of the velum. In contrast, in the sympatric volutid Odontomcymbiola magellanica (Odontocym-biolinae), embryonic development involves three phases: first, slow growth associated to the nutrition resources present in the egg, second, fast growth related to the ingestion of the total solid portion of the intracapsular fluid (major embryo growth), followed by a third phase of slow growth and mostly morphologi-cal changes (Bigatti et al., 2014). In A. ancilla, the velum disappears before hatching, during the coiling embryo stage. The reabsorption was also observed at an equivalent stage of development in the congeneric Adelomelon fer-rusacci (Penchaszadeh & Segade, 2009) and Adelomelon brasiliana (Penchaszadeh, 1999), although in these species, the velum was not measured. The velum size of O. magellanica, is smaller (measured from photographs in Bigatti et al., 2014) than A. ancilla velum. O. magel-lanica reduces it velum before “pediveliger”, while A. ancilla reaches the maximum velum size at that stage. These differences could be related to species differences in feeding be-havior strategies and organ formation during intracapsular development, as was previously described.
In this study, we confirm that the embry-onic growth and organogenesis of A. ancilla is continuous, and is associated with continu-ous intracapsular feeding. However, there is some disagreement regarding embryonic shell growth features (Romero et al., 2004; Bigatti et al., 2014). In A. ancilla, the shell gland was observed at early “pediveliger” stage on the cephalic zone, more specifically in the aperture region of the protoconch, as found by Bigatti et al. (2014). Considering the anterior location of the shell gland it may be interpreted that calcification of the shell in embryos occurs from the aperture zone towards the apex, as was described in O. magellanica (Bigatti et al., 2014). If true, this pattern of calcification dif-fers from that proposed by other authors, who have postulated that calcification within other neogastropod species occurs in the opposite direction (from apex to aperture zone), based on the presence of a posterior cap-like shell gland (D’Asaro, 1966; Romero et al., 2004). In A. an-cilla, the hatchlings showed the apex and other spots lacking calcification (spread around the shell); these areas are subsequently calcified to achieve the final protoconch. This fact might

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support the existence of other calcification ar-eas on the embryo mantle, complementary to the shell gland situated at the aperture zone. Nevertheless, to answer this query, marking experiments of embryos shells (e.g., with calcein) are needed to correctly determine the shell calcification process.
Studies of early intracapsular nutrition by Rivest (1992) have suggested that larval kidneys (= athrocytes; Bigatti et al., 2014) may be related to incorporation of nutrients without ingestion of food through the mouth. The transparent vacuolar cells distinguished on the velum area of A. ancilla could be related to athrocyte cells sensu Bigatti et al. (2014). These cells were recognized at early “veliger” stages of development, mainly situated on the central side ofthe velum. These vacuolar cells have been identified in the sympatric О. magel-lanica (Bigatti et al., 2014), but have not been reported in other published studies of volutid species. This group of cells is commonly re-ported as larval kidneys in the literature (Rivest, 1992): an example of this is the nassarid B. globulosus, which inhabits the same area ofA . ancilla (Averbuj et al., 2014). Morphological and experimental evidence supports that the large cell size is related to endocytotically absorbed intracapsular proteins and not to stored waste products (Rivest, 1992). Athrocytes cells are present at early stages and resorption occurs during intracapsular metamorphosis in all the neogastropods examined that hatch as juveniles (Rivest, 1992; Averbuj et al., 2014; Bigatti et al., 2014); probably the same could be occurring in A. ancilla serving in early nutri-ent absorption.
The importance of the amount of extraem-bryonic food sources during development has been discussed by several authors (Fioroni, 1982; Miloslavich, 1996b; Penchaszadeh & Miloslavich, 2001). Abundant intracapsular food in each egg capsule of Adelomelon ancilla might explain the similar size of embryos within an egg capsule (embryos rarely differed in size and/or development stage in the same egg capsule). Food would not be a limiting resource allowing the embryos to feed without competi-tion. Moreover, since there was no indication of a decrease in the number of embryos during development, one might conclude that there is no sibling cannibalism. The egg capsules found in the Volutidae are among the largest recorded for caenogastropods (Penchaszadeh et al., 1999), and possibly contain more nutrients

than species from other families (Penchasza-deh & Miloslavich, 2001). As an example, biochemical intracapsular liquid analysis of Voluta musica demonstrated that there was enough protein and sugar to support its total development (Penchaszadeh & Miloslavich, 2001). In A. ancilla, embryos remained within the egg capsule for a few days after hatching, feeding of the remnant intracapsular food by grasping the internal walls by the radula. In contrast, however, in O. magellanica, intraca-psular food is ingested quickly by embryos, which suggests the existence of intracapsular competition (Bigatti et al., 2014). Smith & Thatje (2013) proposed that the modality and speed of intracapsular ingestion are determinants of sibling feeding competition. Nonetheless, as this two species (e.g. the sympatric A. ancilla and O. magellanica) belong to different sub-families, these developmental differences may be phylogenetic.
The embryonic developmental time in A. ancilla was estimated between 5-6 months. This is much longer than those recorded for the volutids O. magellanica: 2-3 months (Bigatti et al., 2014) and Z. dufresnei: 35 days (Roche et al., 2013.) in the northern gulfs of Patagonia. Developmental times are often correlated with embryos size (Spight, 1975). In support of this, the few hatchling embryos of A. ancilla achieved a much larger average size (10.4 mm in shell length) compared with О. magellanica (8.9 mm in shell length). It is widely assumed that offspring quality increases with size (e.g., Thorson, 1950; Gosselin & Rehak, 2007; Lloyd & Gosselin, 2007; Przeslawski, 2011). Therefore, the larger A. ancilla hatchlings are less likely to be affected by such factors as physical stress, predation and starvation (Smith & Thatje, 2013).
The neogastropod A. ancilla has an ecologi-cal significance in Patagonian shallow waters communities, defined by its high trophic position as a top predator in benthic food webs (Zabala et al., 2013a). The results of the present study: direct development, long developmental time (5-6 months) and presence of few embryos inside each egg capsule, denote the fragility of this species as stated previously on basis of such population parameters as longevity, very low density and late reproductive maturity (Pen-chaszadeh et al., 2009; Zabala et al., 2013b). All this features indicate that A. ancilla is not a recommendable resource for commercial exploitation in Nuevo gulf populations.

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